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ENVIRONMENTAL CAPACITY - THE CONTENT OF THE CONCEPT AND ITS APPLICATION IN ECOLOGY

By V.E. Zaika

The concept of "environmental capacity" in Soviet ecological literature is borrowed from the English (*carrying capacity, environmental capacity)* primarily owing to the translation into Russian of major monographs and manuals on ecology [1 - 3]. This concept will undoubtedly be useful in certain fields of ecology. At the same time it remains so far only fleetingly outlined and to avoid equivocal interpretations it must be defined more substantially. This is the goal of the present discussion.

What is "environmental capacity"? It is usually mentioned when analyzing the limits of population growth [1,2, 4 - 6], meaning that a population cannot exceed some maximal density which is "allowable" in a given habitat given the observed complex of conditions. In accordance with this [3], environmental capacity is defined as the number of individuals whose needs can be satisfied by the resources of a given habitat. This definition clearly indicates the nature of the phenomenon, but embraces only a part of what is comprehended by environmental capacity in different fields of contemporary ecology.

In the first place, a limit of growth is attained in a specific environment both for a population as well as for any other ecological grouping in which the investigator is interested. In studying size groups, taxocenes or individual trophic links in biocoenoses, the ecologist always observes a limitation of their development in a given environment. Therefore, it is desirable that environmental capacity be applicable to any biosystems, and not only to populations.

However, the term should not be limited only to biosystems, since the requirement for such a concept is also felt in the study of nonliving links in ecosystems. For example, the expressions "phosphate capacity of the environment" and "environmental capacity with respect to pollution"are already being used in the literature. Understandably, in such a situation, the concept of environmental capacity can have different interpretations, which will lead to misunderstandings. It is therefore necessary to standardize the application of the concept on the basis of a definition which will permit its unequivocal use in different fields of ecology.

Secondly, when discussing biosystems, environmental capacity should not be considered measurable only by the number of individuals. The limitation mechanism often "rests" on biomass or on functional variable biosystems (such as total food consumption, metabolism, production), that is, incoming and outgoing material flows. Essentially, environmental capacity can be measured using any such indicator, but deep analysis of the growth limitation mechanisms is most likely possible only when several variables are taken into account simultaneously.

It must be kept in mind that populations and many types of biocoenoses are limited not only by the physical but also by the biotic environment. Therefore, if

we want the concept of environmental capacity to "work well" in helping to analyze ecological processes, then by environment we should understand the entire ecosystem of which the study biosystem is a part. Incidentally, although habitat is often used to mean only the physical environment of the study organisms, a fuller knowledge of their demands on the environment is reached when not only the physical components but the entire ecosystem, including biotic variables, is studied. In other words, the habitat of a species is nothing else than the ecosystem in which it exists as a component. As we know, the environment is completely abiotic only in relation to biocoenoses which include everything living in the given ecosystem.

In discussing environmental capacity with respect to nonliving components, it also must be measured in terms analogous to abundance and biomass. When necessary, one can refer to the magnitude of input and output flows. Here as well, the entire ecosystem of which the study component is a part must be understood as the environment.

On the basis of the above, we arrive at the following definition: environmental capacity is the capacity of a specific ecosystem with respect to the study component measured by means of indicators of content of the component (concentration, density, mass, etc.) or correlated functional variables.

Since a brief definition does not preclude different interpretations, it useful to make some qualifications.

The content of any component in ecosystems is subject to variation, but this variation is not unlimited. Steady states of ecosystems presume the maintenance

of a mobile equilibrium between components in terms of both mass and flows. Environmental capacity with respect to the study component of an ecosystem can be determined only by taking into account the steady state; transitional processes do not yield full information on environmental capacity.

The transition from one steady state to another can be accompanied by considerable change in environmental capacity with respect to the study component. This phenomenon is observed for example in the swamping of lakes, the encroachment of the forest onto the steppe, etc. But here we have in fact a succession of ecosystems. It would seem that this should not be considered when discussing environmental capacity. However, anthropogenic impacts on the environment, particulary to increase its capacity, often lead to a succession of ecosystems, so that one should not lose sight of the relationship between these phenomena.

In analyzing environmental capacity, the ecosystem must be taken in certain spatial limits. All the basic abiotic and biotic variables (environmental factors) must be taken into consideration. So, in order to answer the question: how many rabbits can exist in 1 km^2 of space? - we must know not only the climatic and other physical conditions of the locale, but also the nature of vegetation, the composition and abundance of predators, etc.

Environmental capacity is evaluated by the maximal value of the index used of the development of a component of the ecosystem, but here one should use relatively stable maximums, that is, those which recur regularly or are observed over a long time. Consequently, we are not dealing with random accumulations of

matter or flare-ups in the development of organisms, although analysis of the latter gives a more complete picture of environmental capacity.

Field of applicability of the concept. Without pretending to completeness, let us some examine some of the directions in ecology where the use of the concept of "environmental capacity" is undoubtedly of use.

First of all, this concept is used in discussing the limits of population growth. In all cases when the population growth curve shows "saturation" - an inhibition of growth which approaches asymptotically the abundance or biomass at the upper limit, it is this limit which reflects environmental capacity. In the familiar logistical equation

$$\frac{dN}{dt} = rN\frac{(K-N)}{K}$$

(N is abundance, r is the growth coefficient), which is often used to describe an S-shaped curve of population growth, the value K reflects the upper limit of growth, the maximum possible abundance of the population, that is, K reflects the environmental capacity [2, 3]. The environmental capacity K characterizes that equilibrium state of the biosystem when the birth and death rates are equal.

Population size is regulated by the correlation between the inherent growth potential of a population and the limitations imposed on this growth by the environment. If the problem arises in the study of population growth of determining the upper limit, then comparison of different species or of a single species in different habitats should be based on K, calling it the environmental capacity. Moreover, one should not associate K only with the logistical equation.

The concept of environmental capacity is also useful in analysing the influence of the density of populations (and other biosystems) on their morphological ("structural") and functional features. The question as to the role of factors which are dependent and independent of population density, which has been widely discussed in the literature, has a direct logical connection with the concept of environmental capacity , which reflects the limits of development of a biosystem. In fact, the influence of density is most evident in those cases when the growth of the biosystem has brought it close to exhaustion (fullness) of the environmental capacity. For this reason, it is desirable to study the role of density in evaluating the extent of realization of environmental capacity by a biosystem in each particular situation. The equation cited is usually used in studying species which colonize a given habitat, so that one can judge the value of K from the growth curve only by tracing all stages of colonization (right up to "saturation" of the environment).

Comparison of species by the parameters of the equation shows up different phylogenetic tendencies: maximization of r is evolutionally advantageous in some lines (such groups and species are called r-strategists), while an increase in K is observed in others (K-strategists). Thus the concept of environmental capacity is also enlisted in the discussion of certain problems in evolution.

Of course, the determination of the attainable limit of development of a biosystem on the basis of any acceptable indicators does not exhaust the study of environmental capacity, but does provide initial information about it. It is further necessary to determine what precisely determines environmental capacity, the

capacity of an ecosystem. Here begins an important field of ecology - the problem of limiting factors, change in limitation, and the mechanisms of this phenomenon. Knowing that the equilibrium state is achieved owing to change in the birth and death rates, the ecologist has now to determine what specific factors limit the birth rate and increase the death rate in different conditions, as the value of K is approached. And it is here that the concept of environmental capacity can be very effective.

The term "environmental capacity" which has begun to be used in hydrobiology in the study of biogenic elements suggests that the concept holds promise for the analysis of the kinetics of a number of inert components of ecosystems, whose concentration is clearly connected with the functioning of systems on an ecological time scale. In aqueous ecosystems, such components may be biogenic salts, dissolved organic matter and detritus (this is true for the last two components at least with respect to the biochemically active parts).

The concept of environmental capacity looks quite different when applied to the study of pollution. In such problems, environmental capacity is definitely tied in with the self-cleaning capacity of ecosystems and the nature of involvement of the pollutant in the matter-energy conversion cycle. Apparently, the concept of environmental capacity can also be useful here in molysmology. In any case, its relationship to the concept of "maximum load" should be discussed.

Since up to now, environmental capacity has been discussed in the literature mainly with respect to biosystems, particularly populations, we shall henceforth confine ourselves to biosystems without mentioning that what has been said largely

also applies to inert components of ecosystems.

In the most general terms, it can be said that the capacity of an ecosystem to sustain the existence of any of its component biosystems depends on climate, the composition of the ecosystem and the resources which sustain the study biosystem. Hence it follows that environmental capacity can also be usefully enlisted in discussing the problem of resources in many of its aspects. In particular, in studying the living resources of nature in the interests of humanity, in predicting their reserve and reproduction, in planning artificial changes in ecosystems for the purpose of improving the yield of resources - in all these directions of resource studies, it is necessary to have a clear picture of the existing or expected environmental capacity . Improving environmental capacity is an important method of improving the productivity of ecosystems. It is achieved by removal of a limitation, which leads to an increase in the value of *K*. Such agricultural and fisheries measures as fertilization, irrigation, supplementary feeding, snow retention, creation of greenhouses, etc., are based on this. The removal of a limitation is also achieved by changing the composition of living components of an ecosystem (removal of competitors - "weeds" and control of pathogens). On the other hand, acclimatization and breeding improve the resource yield by the introduction of a species (form) which makes more effective use of the potentials of the ecosystem. In other words, forms are selected for which the capacity of the same ecosystem is higher than for their ecological analogs.

Environmental capacity in connection with the type of study biosystem and ecosystem. Environmental capacity must be studied within definite space and time

limits, the selection of which depends on the type both of the study biosystem and the corresponding ecosystem.

Let us say that the ecologist is interested in environmental capacity with respect to the population of a species which forms aggregations. If K is determined then on the basis of the density which is achieved directly in the aggregations (in ant hills, in hives, at bird rookeries, in swarms of insects and water crustaceans, in schools of fishes), then the K values obtained cannot be considered to be the environmental capacity for the entire species population.

In such cases, the study biosystem is essentially not the population, but some component of it. Such components usually turn out to be qualitatively different stages of ontogenesis, size-age groups or spatial parts of the population occupying different parts of the habitat.

In a heterogeneous environment or for heterotopic species with a complex life cycle which includes metamorphoses and an alternation of sexual and asexual generations, such population components are especially autonomous. The possibility in principle of autonomous study of environmental capacity with respect to each component shows that a study system can well be a part of a population, an intrapopulation group.

If the problem is to study an entire population, then it is necessary to synthesize the data on the environmental capacity with respect to all of its components. In this case, the population must be considered within the spatial limits which ensure all aspects of its existence. The problem then reduces to the study of which life stages of the species (and in what parts of the ecosystem) are

"critical", that is, on which areas of space, by what factors and at what level the development of the species is limited. It is important here to include all reproduction sites, as well as foraging, growth and wintering zones, etc.

The requirements with respect to time boundaries are similar: the investigation must include the characteristic time of existence of the biosystem. For a species population, this means that it is necessary to study the system throughout its life cycle, or more precisely, for a period comparable in duration with the life of one or several generations. In fact, it has been clearly shown by the example of perennial fishes, to what extent the state of a population depends on the periodicity of alternation of productive and poor generations. A profound understanding of environmental capacity requires that such phenomena be taken into account.

Seasonal changes in environmental capacity in many cases are quite obvious, depending on differences in the condition of the physical environment and resources. For species with a rapid alternation of generations (bacteria, protozoans, microalgae), even diurnal changes in environmental capacity should be taken into account.

The study biosystem may be not only a population or a part of it, but also a biocoenosis of different complexity. In solving a number of ecological problems, it is important to know, for example, how much macrobenthos, how many phytophagous animals, soil insects or bacteria a given ecosystem can "contain" and sustain. Such biocoenoses may be taxocenes, size and trophic groupings etc.

In studying environmental capacity with respect to biocoenoses, it is

important to determine what components and links inhibit the development of the whole system, as well as what factors are limiting. It is known that a change in the composition and ratio of species in biocoenoses also changes the environmental capacity. It is therefore useful to know these functions in order to better evaluate the possible limits of development of a biocoenosis of a given type. Determination of environmental capacity with respect to a biocoenosis which includes everything living in the given ecosystem is of definite interest. It has already been mentioned that it is only in this case that the environment is represented only by abiotic components and that this leads to a unique evaluation of environmental capacity with respect to such systems.

Some approaches to the study of environmental capacity. Let us examine a case of study of environmental capacity with respect to a definite species using a single indicator - concentration (abundance) of organisms. By determining at a different time the concentration of the species in the biotope and the limiting factors, we estimate the maximum attainable (and stable) concentration N_{max}, which we take as an index of capacity ($K = N_{max}$).

A sufficiently thorough investigation enables prediction of the value of K given different combinations of conditions, which is facilitated by the study of the species in different biotopes. In many cases it is possible to predict what specific changes in the ecosystem will cause an increase in environmental capacity to a value considerably surpassing the registered N_{max}.

In this connection, it is useful to introduce the concept of the real (K) and potential (K') environmental capacity. The real environmental capacity is that

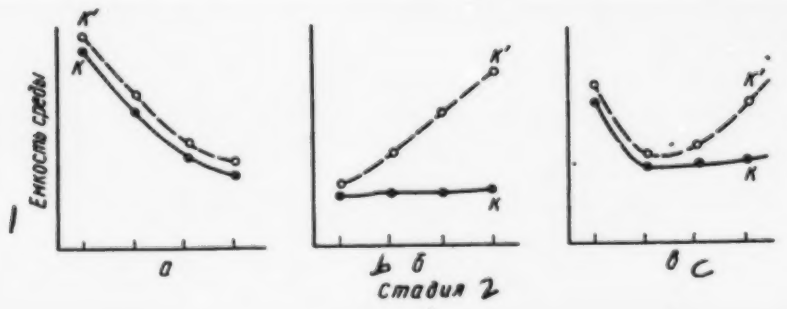

Fig. 1. **Change in environmental capacity (by abundance) with respect to successive size-age groups of a population:**
a **-** simultaneous changes in the potential (*K'*) and real (*K*) environmental capacity; ***b*** **and** ***c*** **-** the abundance of the population is limited at one of the early stages, so that the real environmental capacity for the older stages is below the potential environmental capacity. 1 - environmental capacity; 2 - stage.

which is actually registered in an ecosystem during observations. The potential environmental capacity can be attained in the case of certain natural or artificial changes in the system, so that $K' > K$.

In the majority of species of multicellular animals, the relationship with the environment, the demand for resources and the position in the biocoenosis - in the food chain, "the pyramid of biomasses", etc., change at successive stages in ontogenesis. This indicates that different age groups in populations are often limited by different factors and at different levels of quantitative development. In other words, the capacity of one and the same environment (ecosystem) is different for different stages of the same species.

This leads to the situations which are schematically depicted in Fig. 1. For

each stage in ontogenesis, the ecosystem can show different K and K'. In terms of concentration of organisms, this diagram is explained as follows: the potential environmental capacity here reflects the number of individuals of a given stage which the ecosystem can provide with all required resources and conditions, but the real environmental capacity turns out to be lower in all cases when the abundance of the population is limited at one of the preceding stages of development. Therefore, in order to reach the potential environmental capacity for a particular stage, it is necessary to remove the limitation at the preceding stages. The rearing of young fish at fish farms with subsequent release into bodies of water, for example, serves this purpose.

In this case (Fig. 1), the environmental capacity is compared for each isolated stage of ontogenesis (for different age groups of the population). Then what is the environmental capacity for the whole population? In some cases, we can use the total K for all the stages, that is, the maximal total abundance of individuals: $K = \Sigma K_i = N_{max}$. In applied cases, when the source of the useful bioproduct is a particular stage, its abundance is taken as a basis and possible ways of increasing environmental capacity with respect to just this stage are analyzed. Then the other stages are considered only to the extent necessary to solve the basic problem. Thus, if the bioproduct comes from the early stages of development, then the sexually mature individuals are important as a source of a sufficient amount of young ("brood stock").

Let us now examine a situation where different indicators of environmental capacity are used in analyzing the age groups of a population: in order to

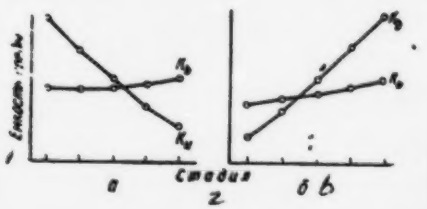

Fig. 2. **Change in environmental capacity in terms of abundance (K_N) and biomass (K_b) :**
a **- the biomass level is limited, which leads to a reduction in K_N in subsequent size groups;** *b* **- the abundance level is limited, so that K_b can increase in subsequent groups. 1 - environmental capacity ; 2 - stage.**

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simplify, we shall take only two indicators - abundance and biomass (Fig. 2). The greater the definitive dimensions of organisms, the more significantly do conclusions diverge with respect to environmental capacity drawn on the basis of different indicators. This is because the role of the age structure of the population becomes increasingly important with increase in the definitive dimensions. In fact, for bacteria or infusoria, the use of abundance, biomass or any functional indicator will given a similar conclusion about environmental capacity. For molluscs or fishes, the total abundance of the population (including larvae) does not provide full information when the ratio of different age groups is not known. Therefore, depending on the problem, one indicator may prove to be more suitable than another for analysing environmental capacity . As has already been mentioned, it is useful to study several variables at the same time since this

facilitates analysis of the mechanisms limiting environmental capacity.

The most important applied research problem in this area is the evaluation of methods and possible limits of artificial increase in environmental capacity. It is precisely in the solution of such problems that the concept of environmental capacity is most useful. These problems are solved by a search for the stages (components) which are limited and the limiting factors with a subsequent selection of methods of removing the limitation.

The sequential removal of a limitation can gradually increase K considerably by comparison with the natural K. A succession of limiting factors and limited stages ("bottlenecks") is observed here, so that adequate means of increasing environmental capacity must be sought each time. Removal of a limitation for many factors at the same time practically means optimization of the ecosystem "in favor" of the component in which we are interested. When such transformations reach a substantial extent, quantitative changes become qualitative - in fact, man is replacing the ecosystem by a new one. At the limit, efforts result in the creation of a cultivator, in which the maximum possible specific environmental capacity is ensured with respect to the species cultivated.

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ENVIRONMENT CAPACITY: THE CONTENT OF THE NOTION AND ITS APPLICATION IN ECOLOGY

Summary

The applicability of the notion "environment capacity" is substantiated for different branches of ecology. The definition of the notion is suggested. The indices of the environment capacity and requirements to research in this field are considered.